Title: Tree height and hydraulic traits shape growth responses across droughts in a temperate broadleaf forest

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Summary

- As climate change is driving increased drought frequency and severity in many forested regions around the world, mechanistic understanding of the factors conferring drought resistance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and species' traits shape tree growth responses during droughts.

- We analyzed tree-ring records for twelve species that comprise 97% of the woody productivity of the 25.6-ha ForestGEO plot in a broadleaf deciduous forest of northern Virginia (USA) to test hypotheses on how tree height, microenvironment characteristics, and species' traits shaped drought responses across the three strongest regional droughts over a 60-year period (1950 - 2009).

- Individual-level drought resistance decreased with tree height, which was strongly correlated with crown exposure. The potentially greater rooting volume of larger trees did not confer an advantage in sites with low topographic wetness index. Resistance was greater among species whose leaves experienced less shrinkage upon desiccation and lost turgor (wilted) at more negative water potentials.

- We conclude that tree height and hydraulic traits influence growth responses during drought, as recorded in the tree-ring record spanning historical droughts. Thus, these factors can be useful for predicting future drought responses under climate change.

Introduction

Forests play a critical global role in climate regulation (Bonan, 2008), yet there remains enormous uncertainty as to how the terrestrial carbon sink, which is dominated by forests, will respond to climate change (Friedlingstein et al., 2006). An important aspect of this uncertainty lies with physiological responses of trees to drought (Kennedy et al., 2019). In many forested regions around the world, the risk of severe drought is increasing (Trenberth et al., 2014; Dai et al., 2018), often despite increasing precipitation (Intergovernmental Panel on Climate Change, 2015; Cook et al., 2015). Droughts, intensified by climate change, have been affecting forests worldwide and are expected to continue as one of the most important drivers of forest change in the future (Allen et al., 2010, 2015). Understanding forest responses to drought requires elucidation of how tree size, microenvironment, and species' traits jointly influence individual-level drought resistance, and the extent to which their influence is consistent across droughts. However, it has proven difficult to resolve the many factors affecting tree growth during drought with available forest census data, which only rarely captures extreme drought, and with tree-ring records, which capture multiple droughts but rarely consider the roles of tree size and microenvironment.

Many studies have shown that within species, large trees tend to be more affected by drought. Greater growth reductions for larger trees was first shown on a global scale by Bennett et al. (2015), and subsequent studies have reinforced this finding (*e.g.*, Stovall et al. (2019); Hacket-Pain et al. (2016)). It has yet to be resolved which of several potential underlying mechanisms most strongly shape size trends in drought response. First, tree height may be a primary driver. Taller trees face the biophysical challenge of lifting water greater distances against the effects of gravity and friction (McDowell et al., 2011; McDowell and Allen, 2015; Ryan et al., 2006; Couvreur et al., 2018). Vertical gradients in stem and leaf traits–including smaller and thicker leaves (higher leaf mass per area, LMA), greater resistance to hydraulic dysfunction (*i.e.*, more negative water potential at 50% loss of hydraulic conductivity, more negative P50), and lower hydraulic conductivity at greater heights (Couvreur et al., 2018; Koike et al., 2001; McDowell et al., 2011)–enable trees to become tall (Couvreur et al., 2018). Indeed, tall trees require xylem of greater hydraulic efficiency, such that xylem conduit diameters are wider in the basal portions of taller trees, both within and across species (Olson et al., 2018; Liu et al., 2019), and throughout the conductive systems of angiosperms (*Zak et al. 2010, Olson et al. 2014,2018*). Wider xylem conduits plausibly make large trees more vulnerable to embolism during drought (Olson et al., 2018), and traits conducive to efficient water transport may also lead to poor ability to recover from or re-route water around embolisms (Roskilly et al., 2019). Larger trees may also have lower drought resistance because their crowns tend to occupy more exposed canopy positions, which are associated with higher evaporative demand (**REFS–KAT**)(Kunert et al., 2017). Subcanopy trees tend to fare better specifically due to the benefits of a buffered environment (Pretzsch et al., 2018). Counteracting the liabilities of associated with tall height, large trees tend to have larger root systems, which potentially counteracts some of the biophysical challenges they face by allowing greater access to water. Finally, tree size-related responses to drought can be modified by species' traits and their distribution across size classes (Meakem et al., 2018; Liu et al., 2019). Understanding the mechanisms driving the greater relative growth reductions of larger trees during drought will require sorting out the interactive effects of height and associated exposure, root water access, and species' traits.

Debates have also arisen regarding the traits influencing tree growth responses to drought. Studies in temperate broadleaf forests have observed that ring-porous species showing higher drought tolerance than diffuse-porous species (Friedrichs et al., 2009; Elliott et al., 2015; Kannenberg et al., 2019), but this

distinction would not hold in the global context (*Wheeler et al. 2007, Olson et al. 2020*) and does not resolve differences among the many species within each category. Commonly-measured traits including wood density and leaf mass per area (LMA) have been linked to drought responses in some temperate deciduous forests (Abrams, 1990; Guerfel et al., 2009; Hoffmann et al., 2011; Martin-Benito and Pederson, 2015) and other forest biomes around the world (Greenwood et al., 2017). However, in other cases these traits could not explain drought tolerance (Maréchaux et al., 2019), or the direction of response was not always consistent. For instance, higher wood density has been associated with greater drought resistance at a global scale (Greenwood et al., 2017), but it correlated negatively with tree performance during drought in a broadleaf deciduous forest in the southeastern United States (Hoffmann et al., 2011). Thus, the perceived influence of these traits on drought resistance may actually reflect indirect correlations with other traits that more directly drive drought responses (Hoffmann et al., 2011). Recent work has shown a great potential for hydraulic traits to predict growth and mortality responses. Hydraulic traits including water potentials at which percent loss of conductivity surpass a certain threshold ($P50$, $P80$, $P88$) and hydraulic safety margin correlate with drought performance (Anderegg et al., 2018) but are time-consuming to measure and therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics). More easily measurable leaf hydraulic traits with direct linkage to plant hydraulic function can explain greater variation in plant distribution and function (Medeiros et al., 2019). These include leaf area shrinkage upon desiccation (PLA_{dry}) (Scoffoni et al., 2014) and the leaf water potential at turgor loss point (π_{tlp}), *i.e.*, the water potential at which leaf wilting occurs (Bartlett et al., 2016). The abilities of both PLA_{dry} and π_{tlp} to explain tree performance under drought remains untested.

Here, we examine how tree height, microenvironment characteristics, and species' traits collectively shape drought responses. We test a series of hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from three droughts (1966, 1977, 1999), species functional and hydraulic trait measurements, and census data from a large forest dynamics plot in Virginia, USA. First, we focus on the role of tree size and its interaction with microenvironment. We examine the contemporary relationship between tree height and microenvironment, including growing season meteorological conditions and crown exposure. We then test whether, consistent with most forests globally, larger-diameter, taller trees tend to have lower drought resistance (Rt) in this forest, which is in a region (eastern North America) represented by only two studies in the global review of Bennett et al. (2015). We also test for an influence of potential access to available soil water, which should be greater for larger trees in dry but not in perpetually wet microsites. Finally, we focus on the role of species' functional and hydraulic traits, testing the hypothesis that species' traits–particularly leaf hydraulic traits–predict Rt. We test predictions that drought resistance is higher in ring-porous than semi-ring and diffuse-porous species, that it is correlated with wood density–either postively (Greenwood et al., 2017) or negatively (Hoffmann et al., 2011)– and positively correlated with LMA, and that hydraulic leaf traits including PLA_{dry} and π_{tlp} are better predictors.

Materials and Methods

Study site and microclimate

Research was conducted at the 25.6-ha ForestGEO (Forest Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W; Fig. **S1**) (Bourg et al., 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains near the northern boundary of Shenandoah National Park. Elevations range from 273 to 338 m above sea

level with a topographic relief of 65m (Bourg et al., 2013). Climate is humid temperate, with mean annual temperature of 12.7°C and precipitation of 1005 mm during our study period (1960-2009; source: CRU TS v.4.01; Harris et al. (2014)). Dominant tree taxa within this secondary forest include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.; Table 2).

To characterize how environmental conditions vary with height, data were obtained from the NEON tower located <1km from the study area via the neonUtilities package (?). We used wind speed, relative humidity, and air temperature data, all measured over a vertical profile spanning heights from 7.2 m to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 (NEON, 2018). After filtering for missing and outlier values, we determined the daily minima and maxima, which we then aggregated at the monthly scale. **(work on organization of this.)**

Identifying drought years

We identified the three largest droughts within the time period 1950-2009, defining drought (Slette et al., 2019) as events with anomalously dry peak growing season climatic conditions. Specifically, we used the metric of Palmer Drought Severity Index (PDSI) during May-August (MJJA; Table S3), which were identified by Helcoski et al. (2019) as the months of the current year to which annual tree growth was most sensitive at this site. PDSI divisional data for Northern Virginia were obtained from NOAA (https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp) in December 2017. Based on this, we identified three drought years - 1966, 1977, and 1999 (Figs. **1**, **S2**, Table S3).

The droughts differed in intensity and antecedent moisture conditions (Fig. **S2**, Table S3). The 1966 drought was preceded by two years of moderate drought during the growing season and severe to extreme drought starting the previous fall and in August reached the lowest growing season $PDSI$ (-4.82) of the three droughts. The 1977 drought was the least intense throughout the growing season, and it was preceded by 2.5 years of near-normal conditions, making it the mildest of the three droughts. The 1999 drought was preceded by wetter than average conditions until the previous June, but reached the lowest PDSI during May-July (-4.53).

Data collection and preparation

Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size, microenvironment characteristics, and species traits (Table 3). The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems ≥ 1cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH and data for all stems ≥ 10cm to analyze functional trait composition relative to tree height (all analyses described below). Census data are available through the ForestGEO data portal (www.forestgeo.si.edu).

We analyzed tree-ring data (xylem growth increment) from 571 trees representing the twelve species with the greatest contributions to woody aboveground net primary productivity ($ANPP_{stem}$), which together comprised 97% of study plot $ANPP_{stem}$ between 2008 and 2013 (Helcoski et al., 2019) (Table 2; Fig. **S1**). Cores (one per tree) were collected within the ForestGEO plot at breast height (1.3m) in 2010-2011 or 2016-2017. In 2010-2011, cores were collected from randomly selected live trees of each species that had at least 30 individuals ≥ 10 cm DBH (Bourg et al., 2013). In 2016-2017, cores were collected from all trees found dead during annual mortality censuses (Gonzalez-Akre et al., 2016). We note that drought was

163 probably not a cause of mortality for these trees, as monthly May-Aug $PDSI$ did not drop below -1.75 in
164 these years or the three years prior (2013-2017), and that trees cored dead displayed similar climate
165 sensitivity to trees cored live (Helcoski et al., 2019). Cores were sanded, measured, and crossdated using
166 standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies (Fig. **1a**) were
167 published in Zenodo (DOI: 10.5281/zenodo.2649302) in association with Helcoski et al. (2019).

168 For each cored tree, we combined tree-ring records and allometric equations of bark thickness to reconstruct
169 DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[\sum_{year=Y}^{2008} (r_{ring,Y}) - r_{bark,Y} + r_{bark,2008} \right]$$

170 Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark
171 thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data
172 from the site (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression on log-transformed
173 data to relate r_{bark} to diameter inside bark from 2008 data (Table S1), which were then used to determine
174 r_{bark} in the DBH reconstruction.

175 Tree heights (H) were measured by several researchers for a variety of purposes between 2012 to 2019
176 (n=1,518 trees). Measurement methods included direct measurements using a collapsible measurement rod
177 on small trees (NEON, 2018) or a tape measure on recently fallen trees (this study); geometric calculations
178 using clinometer and tape measure (Stovall et al., 2018a) or digital rangefinders (Anderson-Teixeira et al.,
179 2015b; NEON, 2018); and ground-based LiDAR (Stovall et al., 2018b). Rangefinders used either the tangent
180 method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights.
181 Both methods are associated with some error (Larjavaara and Muller-Landau, 2013), but in this instance
182 there was no clear advantage of one or the other. Measurements from the National Ecological Observatory
183 Network (NEON) were collected near the ForestGEO plot following standard NEON protocol, whereby
184 vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a
185 rangefinder (NEON, 2018). Species-specific height allometries were developed (Table S2) using logarithmic
186 regression ($ln[H] \sim ln[DBH]$). For species with insufficient height data to create reliable species-specific
187 allometries (n=2, JUNI and FRAM), heights were calculated from an equation developed by combining the
188 height measurements across all species. We then used these allometries to estimate H for each drought year,
189 Y, based on reconstructed DBH_Y.

190 Crown position–a categorical variable classifying trees based on exposure to sunlight–was recorded for all
191 cored trees that remained standing during the growing season of 2018 following the protocol of Jennings et al.
192 (1999). Trees were classified as follows: *dominant* trees were defined as those with crowns above the general
193 level of the canopy, *codominant* trees as those with crowns within the the canopy; *intermediate* trees as those
194 with crowns below the canopy level, but illuminated from above; and *suppressed* as those below the canopy
195 and receiving minimal direct illumination from above.

196 Topographic wetness index (TWI) was calculated using the dynatopmodel package in R (Fig. **S1**) (**?**).
197 Originally developed by Beven and Kirkby (1979), TWI was part of a hydrological run-off model and has
198 since been used for a number of purposes in hydrology and ecology (Sørensen et al., 2006). TWI calculation
199 depends on an input of a digital elevation model (DEM; ~3.7 m resolution from the elevatr package (**?**)), and

from this yields a quantitative assessment defined by how "wet" an area is, based on areas where run-off is more likely. From our observations in the plot, TWI performed better at categorizing wet areas than the Euclidean distance from the stream.

Hydraulic traits were collected in August 2018 (Tables 2-3; Fig. **S4**). We sampled small sun-exposed branches up to eight meters above ground from three individuals of each species in and around the ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and re-hydrated overnight in covered buckets under opaque plastic bags before measurements were taken. Rehydrated leaves taken towards the apical end of the branch (n=3 per individual: small, medium, and large) were scanned, weighed, dried at $60°$ C for $\geq$ 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using the LeafArea R package (Katabuchi, 2019). LMA was calculated as the ratio of leaf dry mass to fresh area. PLA_{dry} was calculated as the percent loss of area between fresh and dry leaves. Wood density was calculated for ~1cm diameter stem samples (bark and pith removed) as the ratio of dry weight to fresh volume, which was estimated using Archimedes' displacement. We used the rapid determination method of Bartlett et al. (2012) to estimate osmotic potential at turgor loss point (π_{tlp}). Briefly, two 4 mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapour pressure osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by the osmometer was used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ (Bartlett et al., 2012).

Statistical Analysis

For each drought year, we calculated drought resistance (Rt) as the ratio of basal area increment (BAI) during drought to the mean BAI over the five years preceding the drought (Lloret et al., 2011). Thus, Rt values <1 and >1 indicate growth reductions and increases, respectively. Because the Rt metric could be biased by directional pre-drought growth trends, we also tried an intervention time series analysis (ARIMA, (**?**)) that predicted mean drought-year growth based on trends over the past ten years and used this value in place of the five-year mean in calculations of resistance (Rt_{ARIMA}= observed BAI/ predicted BAI). The two metrics were strongly correlated (Fig. **S5**). Because Rt tended to produce more reasonable estimates than Rt_{ARIMA} when there was a large difference between these metrics, we selected Rt as our focal metric, presenting parallel results for Rt_{ARIMA} in the Supplementary Info. We focus exclusively on drought resistance (Rt or Rt_{ARIMA}), and not on the resilience metrics described in Lloret et al. (2011), because (1) we would expect resilience to be controlled by a different set of mechanisms, and (2) the findings of *DeSoto et al. (2020)* suggest that Rt is a more important drought response metric for angiosperms.

Analyses focused on testing the predictions presented in Table 1, with Rt (or Rt_{ARIMA}) as the response variable. Models were run for all drought years combined and for each drought year individually. The general statistical model for hypothesis testing was a mixed effects model, implemented in the lme4 package in R [**REF**], with Rt (or Rt_{ARIMA}) as the response variable, tree nested within species as a random effect, and independent variables as specified below. In the multi-year model only, we also included a fixed effect of drought year. (**IAN, CONFIRM THIS**)) We used AICc to assess model selection, and conditional/marginal R-squared to assess model fit as implemented in the AICcmodavg package in R (**?**). AICc refers to a corrected version of AICc, and is best suited for small data sizes (see Brewer et al., 2016).

To avoid over-fitting models with five species traits (Table 3) across only 12 species, we did not include all traits as fixed effects in a single GLMM, but rather conducted individual tests of each species trait to

241 determine the relative importance and appropriateness for inclusion in the main model. These tests followed
242 the model structure specified above, including $ln[H]$, TWI, and crown position in the null model. Trait
243 variables were considered appropriate for inclusion in the main model if they had a consistent direction of
244 response across all droughts and if their addition to this null model lacking the trait improved fit (at ΔAICc
245 ≥ 1.0) in at least one drought year (Table S4). We note that the ΔAICc ≥ 1.0 criterion is not a test of
246 significance, but of whether the variable has enough influence to be considered as a *candidate* variable in full
247 models.

248 We then determined the top full models for predicting Rt (or Rt_{ARIMA}). To do so, we compared models
249 with all possible combinations of candidate variables, including $ln[H]*TWI$ and species traits as specified
250 above. We identified the full set of models within ΔAICc=2 of the best model (that with lowest AICc).
251 When a variable appeared in all of these models and the sign of the coefficient was consistent across models,
252 we viewed this as support for the acceptance/rejection of the associated prediction (Table 1). If the variable
253 appeared in some but not all of these models, and its sign we was consistent across models, we considered
254 this partial support/rejection. In presentation of the results below, we note instances where the Rt_{ARIMA}
255 model disagreed with the Rt model, but otherwise do not discuss the Rt_{ARIMA} model.

256 All analysis beyond basic data collection was performed using R version 3.5.3 (R Core Team, 2020). Other
257 R-packages aside from those already listed were very helpful in conducting analyses. These are listed in the
258 Supplementary Information. All data, code, and results are available through the SCBI-ForestGEO
259 organization on GitHub (https://github.com/SCBI-ForestGEO: SCBI-ForestGEO-Data and
260 McGregor_climate-sensitivity-variation repositories), with static versions corresponding to data and analyses
261 presented here archived in Zenodo (DOIs: 10.5281/zenodo.3604993 and [TBD], respectively.

262 **Results**

263 *Tree height and microenvironment*

264 In the years for which we have vertical profiles in climate data (2016-2018), taller trees–or those in dominant
265 crown positions– were generally exposed to higher evaporative demand during the peak growing season
266 months (May-August; Fig. **2**). Specifically, maximum daily wind speeds were significantly higher above the
267 top of the canopy (40-50m) than within and below (10-30m) (Fig. **2a**). Relative humidity was also somewhat
268 lower during June-August, ranging from ~50-80% above the canopy and ~60-90% in the understory (Fig. **2b**).
269 Air temperature did not vary across the vertical profile (Fig. **2c**).

270 Crown position varied as expected with height (dominant > co-dominant > intermediate > suppressed), but
271 with substantial variation (Fig. **2d**). Correlation between height and canopy position was 0.73.

272 *Community-level and species' drought responses*

273 At the community level, cored trees showed substantial growth reductions in all three droughts, with a mean
274 Rt of 0.86 in 1966 and 1999, and 0.84 in 1977 (Fig. **2b**). Across the entire study period (1950-2009), the
275 focal drought years were the three years with the largest fraction of trees exhibiting $Rt \leq 0.7$. Specifically, in
276 each drought, roughly 30% of the cored trees had growth reductions of $\geq 30\%$ ($Rt \leq 0.7$): 29% in 1966, 32%
277 in 1977, and 27% in 1999. However, some individuals exhibited increased growth, *i.e.*, $Rt > 1.0$: 26% of trees
278 in 1966, 22% in 1977, and 26% in 1999.

279 Responses varied across species and by drought (Fig. **3**). Averaged across all droughts, Rt was lowest in

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280 *Liriodendron tulipifera* (mean $Rt = \mathbf{0.66}$) and highest in *Fagus grandifolia* (mean $Rt = \mathbf{0.99}$).

281 *Tree height, microenvironment, and drought resistance*

282 Taller trees showed stronger growth reductions during drought when evaluating the three drought years
283 together and for 1966 individually (Table 1; Fig. **4**). Specifically, $ln[H]$ appeared, with negative coefficient,
284 in the best models and all top models (Tables S6-S7). For the 1977 drought, $ln[H]$ did not appear in the best
285 model, but was included, with negative coefficient, among the top models–*i.e.*, models that were statistically
286 indistinguishable (ΔAICc<2) from the best model (Tables 1, S6-S7). For the 1999 drought, $ln[H]$ appeared
287 in no top models for Rt and some top models, with positive coefficient, for Rt_{ARIMA}.

288 Rt had a significantly negative response to $ln[TWI]$ in all drought years combined and in 1977 and 1999
289 individually (Fig. 4, Table S6). When Rt_{ARIMA} was used as the response variable, the effect was significant
290 in all drought years combined and in 1977, and a negative effect of $ln[TWI]$ was included in some of the
291 models in 1966 and 1999 (Table S7). This negates the idea that trees in moist microsites would be less
292 affected by drought. Nevertheless, we tested for a $ln[H] * ln[TWI]$ interaction, a negative sign of which could
293 indicate that smaller trees (with smaller rooting volume) are more susceptible to drought in drier
294 microenvironments with a deeper water table. This hypothesis was rejected, as the $ln[H] * ln[TWI]$
295 interaction was never significant, and had a positive sign in any top models in which it appeared (Tables 1,
296 S6-S7). This term did appear, with positive coefficient, in the best Rt_{ARIMA} model for all years combined
297 (Table S7).

298 *Species' traits and drought resistance*

299 Species traits. . . (Table 2, Fig. **S4**)

300 Wood density, LMA, and xylem porosity were all poor predictors of Rt (Tables 1,S4-S5). Wood density and
301 LMA were never significantly associated with Rt in the single-variable tests and were therefore excluded
302 from the full models. Xylem porosity was also excluded from the full models, as it had no significant
303 influence for all droughts combined and had contrasting effects in the individual droughts: whereas
304 ring-porous species had higher Rt than diffuse- and semi-ring- porous species in the 1966 and 1999 droughts,
305 they had lower Rt in 1977 (Table S4). It is noteworthy that the two diffuse-porous species in our study,
306 *Liriodendron tulipifera* and *Fagus grandifolia*, were at opposite ends of the Rt spectrum (Fig. **3**), further
307 refuting the idea that xylem porosity is a useful predictor of Rt in the context of this study.

308 In contrast, PLA_{dry}, and π_{tlp} were linked to drought responses (Fig. **4**; Tables 1,S4-S7). Both had consistent
309 signs across all droughts and explained modest amounts of variation (ΔAICc > 1.0) during at least one of
310 the three droughts (Table S4), qualifying them as candidate variables for the full model. PLA_{dry} had a
311 significant influence, with negative coefficient, in full models for the three droughts combined and for the
312 1966 drought individually (Fig. **4**; Tables S6-S7). For 1977 and 1999, it was included, with negative
313 coefficient, in some of the top models (Tables S6-S7). π_{tlp} was included, with negative coefficient, in the best
314 model for all droughts combined and for the 1977 drought individually (Fig. **4**; Table S6). It was included in
315 some of the top models for 1999 (Tables S6-S7).

Discussion

317 Tree height, microenvironment, and hydraulic traits shaped tree growth responses across three droughts at
318 our study site (Table 1, Fig. **4**). The greater susceptibility of larger trees to drought, similar to forests

worldwide (Bennett et al., 2015), was driven primarily by their height (Stovall et al., 2019). Taller height was likely a liability in itself, and was also associated with greater exposure to conditions that would promote water loss and heat damage during drought (Fig. **2**). There was no evidence that soil water availability increased drought resistance; in contrast, trees in wetter topographic positions had lower Rt (Zuleta et al., 2017; Stovall et al., 2019), and the larger potential rooting volume of large trees provided no advantage in the drier microenvironments. The negative effect of height on Rt held after accounting for species' traits. Drought resistance was not consistently linked to species' LMA, wood density, or xylem type (ring- vs. diffuse porous), but was negatively correlated with leaf hydraulic traits (PLA_{dry}, π_{tlp}). This is the first report to our knowledge linking PLA_{dry} and π_{tlp} to growth reduction during drought. The directions of these responses were consistent across droughts (Table S6), supporting the premise that they were driven by fundamental physiological mechanisms. However, the strengths of each predictor varied across droughts (Fig. **4**; Tables S6-S7), indicating that drought characteristics interact with tree size, microenvironment, and traits to shape which individuals are most affected. These findings advance our knowledge of the factors that make trees vulnerable to growth declines during drought–and, by extension, likely make them more vulnerable to mortality (Sapes et al., 2019).

The droughts considered here were of a magnitude that has occurred with an average frequency of approximately once every 10-15 years (Fig. **1a**, Helcoski et al. (2019)) and had substantial but not devastating impacts on tree growth (Figs. **1b**). These droughts were classified as severe (1977) or extreme (1966, 1999) according to the PDSI metric and have been linked to tree mortality in the eastern United States (Druckenbrod et al., 2019); however, extreme, multiannual droughts or so-called "megadroughts" of the type that have triggered massive tree die-off in other regions (e.g., Allen et al. (2010); Stovall et al. (2019)) have not occurred in the Eastern United States within the past several decades (Clark et al., 2016). Of the droughts considered here, the 1966 drought, which was preceded by two years of dry conditions (Fig. **S2**), severely stressed a larger portion of trees (Fig. **1b**). The tendency for large trees to have lowest resistance was most pronounced in this drought, consistent with other findings that this physiological response increases with drought severity (Bennett et al., 2015; Stovall et al., 2019). Across all three droughts, the majority of trees experienced reduced growth, but a substantial portion had increased growth (Fig. **1b**), potentially due to decreased leaf area of competitors during the drought (**REF–if we can find one**), and consistent with prior observations that smaller trees can exhibit increased growth rates during drought (Bennett et al., 2015). It is likely because of the moderate impact of these droughts, along with other factors influencing tree growth (e.g., stand dynamics), that our best models characterize only a modest amount of variation in Rt: 11-12% for all droughts combined, and 18-25% for each individual drought (Table S6).

Consistent with studies in other forests worldwide (Bennett et al., 2015), taller trees in this forest exhibited lower drought resistance. Mechanistically, this is consistent with, and reinforces, previous findings that biophysical constraints make it impossible for trees to efficiently transport water to great heights and simultaneously maintain strong resistance and resilience to drought-induced embolism (Olson et al., 2018; Couvreur et al., 2018; Roskilly et al., 2019). Taller trees also face dramatically different microenvironments (Fig. **2**). They are exposed to higher wind speeds and lower humidity (Fig. **2a-b**), resulting in higher evaporative demand. Unlike other temperate forests where modestly cooler understory conditions have been documented (*Zellweger et al. 2019*), particularly under drier conditions (*Davis et al. 2019*), we observed no significant variation in air temperatures across the vertical profile (Fig. **2c**). More critically for tree physiology, leaf temperatures can become significantly elevated over air temperature under conditions of high

solar radiation and low stomatal conductance (*Campbell & Norman; Rey-Sanchez et al. 2016*). Under drought, when air temperatures tend to be warmer, direct solar radiation tends to be higher (because of less cloud cover), and less water is available for evaporative cooling of the leaves, trees with sun-exposed crowns may not be able to simultaneously maintain leaf temperatures below damaging extremes and avoid drought-induced embolism. Indeed previous studies have shown lower drought resistance in more exposed trees (Liu and Muller, 1993; Suarez et al., 2004; Scharnweber et al., 2019). Unfortunately, collinearity between height and crown exposure in this study (Fig. **2d**) makes it impossible to confidently partition causality. Additional research comparing drought responses of early successional and mature forest stands, along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

Belowground, taller trees would tend to have larger root systems, but the potentially greater access to water did not override the disadvantage conferred by height–and, in fact, greater moisture access in non-drought years (here, higher TWI) appears to make trees more sensitive to drought (Zuleta et al., 2017; Stovall et al., 2019). The observed height-sensitivity of Rt, together with the lack of advantage to large stature in drier topographic positions, agrees with the concept that physiological limitations to transpiration under drought shift from soil water availability to the plant-atmosphere interface as forests age (Bretfeld et al., 2018), such that tall, dominant trees are the most sensitive in mature forests. Again, additional research comparing drought responses across forests with different tree heights and water availability would be valuable for disentangling the relative importance of above- and belowground mechanisms across trees fo different size.

The development of tree-ring chronologies for the twelve most dominant tree species at our site (Helcoski et al., 2019; Bourg et al., 2013) gave us the sample size to compare historical drought responses across species (Fig. **3**) and associated traits at a single site (see also Elliott et al., 2015). Our study reinforced the findings of previous studies (see Introduction) that wood density and LMA are not reliably linked to drought resistance (Table 1). Contrary to previous studies in temperate deciduous forests, we did not find an association between xylem porosity and drought tolerance, as the two diffuse-porous species, *Liriodendron tulipifera* and *Fagus grandifolia*, were at opposite ends of the Rt spectrum (Fig. **3**). While the low Rt of *L. tulipifera* is consistent with other studies (Elliott et al., 2015), the high Rt of *F. grandifolia* contrasts with studies identifying diffuse porous species in general (Elliott et al., 2015; Kannenberg et al., 2019), and the genus *Fagus* in particular (Friedrichs et al., 2009), as drought sensitive.

There are two potential explanations for this discrepancy. First, other traits can and do override the influence of xylem porosity on drought resistance. Ring porous species are restricted mainly to temperate deciduous forests (*Wheeler et al. 2007*), while highly drought-tolerant diffuse-porous species exist in other biomes (*REFS*). *Fagus grandifolia* had intermediate π_{tlp} and low PLA_{dry} (Fig. **S4**), which would have contributed to it's drought resistance (Fig. **4**; see discussion below). A second explanation of why *F. grandifolia* trees at this particular site had higher Rt is that the sampled individuals, reflective of the population within the plot, are generally shorter and in less dominant canopy positions compared to most other species (Fig. **S4**). The species, which is highly shade-tolerant, also has deep crowns (Anderson-Teixeira et al., 2015b), implying that a lower proportion of leaves would be affected by harsher microclimatic conditions at the top of the canopy under drought (Fig. **2**). Thus, the high Rt of the sampled *F. grandifolia* population can be explained by a combination of fairly drought-resistant leaf traits, shorter stature, and a buffered microenvironment.

Concerted measurement of tree-rings and leaf hydraulic traits of emerging importance (Scoffoni et al., 2014; Bartlett et al., 2016; Medeiros et al., 2019) allowed novel insights into the role of hydraulic traits in shaping

drought response. The finding that PLA_{dry} and π_{tlp} can be useful for predicting drought responses of tree growth (Fig. **4**; Table 1) is both novel and consistent with previous studies linking these traits to habitat and drought tolerance. Previous studies have demonstrated that π_{tlp} and PLA_{dry} are physiologically meaningful traits linked to species distribution along moisture gradients (Maréchaux et al., 2015; Fletcher et al., 2018; Medeiros et al., 2019; Simeone et al., 2019; Rosas et al., 2019), and our findings indicate that these traits also influence drought responses. Furthermore, the observed linkage of π_{tlp} to Rt in this forest aligns with observations in the Amazon that π_{tlp} is higher in drought-intolerant than drought-tolerant plant functional types and adds support to the idea that this trait is useful for categorizing and representing species' drought responses in models (Powell et al., 2017). Because both PLA_{dry} and π_{tlp} can be measured relatively easily (Bartlett et al., 2012; Scoffoni et al., 2014), they hold promise for predicting drought growth responses across diverse forests. The importance of predicting drought responses from species traits increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that do not form annual rings, and for diverse tropical forests. Although progress is being made for the tropics (Schöngart et al., 2017), a full linkage of hydraulic traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (Powell et al., 2017).

As climate change drives increasing drought in many of the world's forests (Trenberth et al., 2014; Intergovernmental Panel on Climate Change, 2015), the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Large trees have been disproportionately impacted by strong drought in forests around the world (Bennett et al., 2015; Stovall et al., 2019), and we show, at least at this site, that this is primarily driven by their height, potentially with some contributions from crown position. The distinction is important because it suggests that height *per se* makes trees vulnerable, even if their crowns are somewhat protected by neighbors, whereas shorter solitary trees or the dominant trees in young forests that recently established after logging or natural disturbances should be less vulnerable. This would suggest that, all else being equal, mature forests would be more vulnerable to drought than young forests with short trees; however, root water access may limit the young forests (Bretfeld et al., 2018), and species traits often shift as forests age. Early- to mid- successional species at our site (*Liriodendron tulipifera*, *Quercus spp.*, *Fraxinus americana*) display a mix of traits conferring drought tolerance and resistance (Table 2), and further research on how hydraulic traits and drought vulnerability change over the course of succession would be valuable for addressing how drought tolerance changes as forests age (e.g. Rodríguez-Catón et al., 2015). In the meantime, the results of this study advance our knowledge of the factors conferring drought resistance in a mature forest, opening the door for more accurate forecasting of forest responses to future drought.

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Author Contribution

KAT, IM, and AJT designed the research. Tree-ring chronologies were developed by RH under guidance of AJT and NP. Trait data was collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.

Supplementary Information

redo this list!!

Table S1: Species-specific bark thickness regression equations

Table S2: Species-specific height regression equations

Table S3: Palmer drought severity index (PDSI) by month for focal droughts

Figure S1: Map of ForestGEO plot showing TWI and location of cored trees

Figure S2: Time series of Palmer Drought Severity Index (PDSI) for the 2.5 years prior to each focal drought

Figure S3: Height (from reconstructed DBH) by crown position across the three focal droughts and in the year of measurement (2018)

References

Abrams, M. D. (1990). Adaptations and responses to drought in Quercus species of North America. *Tree Physiology*, 7(1-2-3-4):227–238.

Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8):art129.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., and Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4):660–684.

Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., and Zenes, N. (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, 561(7724):538–541.

Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Wright, S. J., Salim, K. A., Zambrano, A. M. A., Alonso, A., Baltzer, J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., Chuyong, G. B., Clay, K., Cordell, S., Dattaraja, H. S., Deng, X., Detto, M., Du, X., Duque, A., Erikson,

D. L., Ewango, C. E. N., Fischer, G. A., Fletcher, C., Foster, R. B., Giardina, C. P., Gilbert, G. S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W. W., Hart, T. B., Hau, B. C. H., He, F., Hoffman, F. M., Howe, R. W., Hubbell, S. P., Inman-Narahari, F. M., Jansen, P. A., Jiang, M., Johnson, D. J., Kanzaki, M., Kassim, A. R., Kenfack, D., Kibet, S., Kinnaird, M. F., Korte, L., Kral, K., Kumar, J., Larson, A. J., Li, Y., Li, X., Liu, S., Lum, S. K. Y., Lutz, J. A., Ma, K., Maddalena, D. M., Makana, J.-R., Malhi, Y., Marthews, T., Serudin, R. M., McMahon, S. M., McShea, W. J., Memiaghe, H. R., Mi, X., Mizuno, T., Morecroft, M., Myers, J. A., Novotny, V., Oliveira, A. A. d., Ong, P. S., Orwig, D. A., Ostertag, R., Ouden, J. d., Parker, G. G., Phillips, R. P., Sack, L., Sainge, M. N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H. S., Tan, S., Thomas, S. C., Thomas, D. W., Thompson, J., Turner, B. L., Uriarte, M., Valencia, R., Vallejo, M. I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., and Zimmerman, J. (2015a). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21(2):528–549.

Anderson-Teixeira, K. J., McGarvey, J. C., Muller-Landau, H. C., Park, J. Y., Gonzalez-Akre, E. B., Herrmann, V., Bennett, A. C., So, C. V., Bourg, N. A., Thompson, J. R., McMahon, S. M., and McShea, W. J. (2015b). Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology*, 29(12):1587–1602.

Bartlett, M. K., Klein, T., Jansen, S., Choat, B., and Sack, L. (2016). The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences*, 113(46):13098–13103.

Bartlett, M. K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K., and Sack, L. (2012). Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution*, 3(5):880–888.

Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1(10):15139.

Beven, K. J. and Kirkby, M. J. (1979). A physically based, variable contributing area model of basin hydrology / Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. *Hydrological Sciences Bulletin*, 24(1):43–69.

Bonan, G. B. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, 320(5882):1444–1449.

Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C., and Shen, X. (2013). Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot. *Ecology*, 94(9):2111–2112.

Bretfeld, M., Ewers, B. E., and Hall, J. S. (2018). Plant water use responses along secondary forest succession during the 2015–2016 El Niño drought in Panama. *New Phytologist*, 219(3):885–899.

Brewer, M. J., Butler, A., and Cooksley, S. L. (2016). The relative performance of AIC, AICC and BIC in the presence of unobserved heterogeneity. *Methods in Ecology and Evolution*, 7(6):679–692.

Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., D'Amato, A. W., Davis, F. W., Hersh, M. H., Ibanez, I., Jackson, S. T., Matthews, S., Pederson, N., Peters, M., Schwartz, M. W.,

518 Waring, K. M., and Zimmermann, N. E. (2016). The impacts of increasing drought on forest dynamics,
519 structure, and biodiversity in the United States. *Global Change Biology*, 22(7):2329–2352.

520 Condit, R. (1998). *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama*
521 *and a Comparison with Other Plots.* Springer Berlin Heidelberg, Berlin, Heidelberg.

522 Cook, B. I., Ault, T. R., and Smerdon, J. E. (2015). Unprecedented 21st century drought risk in the
523 American Southwest and Central Plains. *Science Advances*, 1(1):e1400082.

524 Couvreur, V., Ledder, G., Manzoni, S., Way, D. A., Muller, E. B., and Russo, S. E. (2018). Water transport
525 through tall trees: A vertically explicit, analytical model of xylem hydraulic conductance in stems. *Plant,*
526 *Cell & Environment*, 41(8):1821–1839.

527 Dai, A., Zhao, T., and Chen, J. (2018). Climate Change and Drought: a Precipitation and Evaporation
528 Perspective. *Current Climate Change Reports*, 4(3):301–312.

529 Druckenbrod, D. L., Martin-Benito, D., Orwig, D. A., Pederson, N., Poulter, B., Renwick, K. M., and
530 Shugart, H. H. (2019). Redefining temperate forest responses to climate and disturbance in the eastern
531 United States: New insights at the mesoscale. *Global Ecology and Biogeography*, 28(5):557–575.

532 Elliott, K. J., Miniat, C. F., Pederson, N., and Laseter, S. H. (2015). Forest tree growth response to
533 hydroclimate variability in the southern Appalachians. *Global Change Biology*, 21(12):4627–4641.

534 Fletcher, L. R., Cui, H., Callahan, H., Scoffoni, C., John, G. P., Bartlett, M. K., Burge, D. O., and Sack, L.
535 (2018). Evolution of leaf structure and drought tolerance in species of Californian Ceanothus. *American*
536 *Journal of Botany*, 105(10):1672–1687.

537 Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M.,
538 Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K.,
539 Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R.,
540 Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N. (2006). Climate–Carbon Cycle Feedback
541 Analysis: Results from the C4MIP Model Intercomparison. *Journal of Climate*, 19(14):3337–3353.

542 Friedrichs, D. A., Trouet, V., Büntgen, U., Frank, D. C., Esper, J., Neuwirth, B., and Löffler, J. (2009).
543 Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees*, 23(4):729.

544 Gonzalez-Akre, E., Meakem, V., Eng, C.-Y., Tepley, A. J., Bourg, N. A., McShea, W., Davies, S. J., and
545 Anderson-Teixeira, K. (2016). Patterns of tree mortality in a temperate deciduous forest derived from a
546 large forest dynamics plot. *Ecosphere*, 7(12):e01595.

547 Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R.,
548 Laughlin, D. C., Kattge, J., Bönisch, G., Kraft, N. J. B., and Jump, A. S. (2017). Tree mortality across
549 biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*,
550 20(4):539–553.

551 Guerfel, M., Baccouri, O., Boujnah, D., Chaïbi, W., and Zarrouk, M. (2009). Impacts of water stress on gas
552 exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (Olea
553 europaea L.) cultivars. *Scientia Horticulturae*, 119(3):257–263.

554 Hacket-Pain, A. J., Cavin, L., Friend, A. D., and Jump, A. S. (2016). Consistent limitation of growth by

555 high temperature and low precipitation from range core to southern edge of European beech indicates
556 widespread vulnerability to changing climate. *European Journal of Forest Research*, 135(5):897–909.

557 Harris, I., Jones, P. D., Osborn, T. J., and Lister, D. H. (2014). Updated high-resolution grids of monthly
558 climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3):623–642.

559 Helcoski, R., Tepley, A. J., Pederson, N., McGarvey, J. C., Meakem, V., Herrmann, V., Thompson, J. R.,
560 and Anderson-Teixeira, K. J. (2019). Growing season moisture drives interannual variation in woody
561 productivity of a temperate deciduous forest. *New Phytologist*, 0(0).

562 Hoffmann, W. A., Marchin, R. M., Abit, P., and Lau, O. L. (2011). Hydraulic failure and tree dieback are
563 associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*,
564 17(8):2731–2742.

565 Intergovernmental Panel on Climate Change (2015). *Climate Change 2014: Impacts, Adaptation and*
566 *Vulnerability: Working Group II Contribution to the IPCC Fifth Assessment Report. Volume 2 Volume 2.*
567 OCLC: 900892773.

568 Jennings, S. B., Brown, N. D., and Sheil, D. (1999). Assessing forest canopies and understorey illumination:
569 canopy closure, canopy cover and other measures. *Forestry: An International Journal of Forest Research*,
570 72(1):59–74.

571 Kannenberg, S. A., Novick, K. A., Alexander, M. R., Maxwell, J. T., Moore, D. J. P., Phillips, R. P., and
572 Anderegg, W. R. L. (2019). Linking drought legacy effects across scales: From leaves to tree rings to
573 ecosystems. *Global Change Biology*, 0(ja).

574 Katabuchi, M. (2019). *LeafArea: Rapid Digital Image Analysis of Leaf Area*. R package version 0.1.8.

575 Kennedy, D., Swenson, S., Oleson, K. W., Lawrence, D. M., Fisher, R., Costa, A. C. L. d., and Gentine, P.
576 (2019). Implementing Plant Hydraulics in the Community Land Model, Version 5. *Journal of Advances in*
577 *Modeling Earth Systems*, 11(2):485–513.

578 Koike, T., Kitao, M., Maruyama, Y., Mori, S., and Lei, T. T. (2001). Leaf morphology and photosynthetic
579 adjustments among deciduous broad-leaved trees within the vertical canopy profile. *Tree Physiology*,
580 21(12-13):951–958.

581 Kunert, N., Aparecido, L. M. T., Wolff, S., Higuchi, N., Santos, J. d., Araujo, A. C. d., and Trumbore, S.
582 (2017). A revised hydrological model for the Central Amazon: The importance of emergent canopy trees in
583 the forest water budget. *Agricultural and Forest Meteorology*, 239:47–57.

584 Larjavaara, M. and Muller-Landau, H. C. (2013). Measuring tree height: a quantitative comparison of two
585 common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, 4(9):793–801.

586 Liu, H., Gleason, S. M., Hao, G., Hua, L., He, P., Goldstein, G., and Ye, Q. (2019). Hydraulic traits are
587 coordinated with maximum plant height at the global scale. *Science Advances*, 5(2):eaav1332.

588 Liu, Y. and Muller, R. N. (1993). Effect of Drought and Frost on Radial Growth of Overstory and
589 Undesrstory Stems in a Deciduous Forest. *The American Midland Naturalist*, 129(1):19–25.

590 Lloret, F., Keeling, E. G., and Sala, A. (2011). Components of tree resilience: effects of successive
591 low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12):1909–1920.

Martin-Benito, D. and Pederson, N. (2015). Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *Journal of Biogeography*, 42(5):925–937.

Maréchaux, I., Bartlett, M. K., Sack, L., Baraloto, C., Engel, J., Joetzjer, E., and Chave, J. (2015). Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest. *Functional Ecology*, 29(10):1268–1277.

Maréchaux, I., Saint-André, L., Bartlett, M. K., Sack, L., and Chave, J. (2019). Leaf drought tolerance cannot be inferred from classic leaf traits in a tropical rainforest. *Journal of Ecology*.

McDowell, N. G. and Allen, C. D. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, 5(7):669–672.

McDowell, N. G., Bond, B. J., Dickman, L. T., Ryan, M. G., and Whitehead, D. (2011). Relationships Between Tree Height and Carbon Isotope Discrimination. In Meinzer, F. C., Lachenbruch, B., and Dawson, T. E., editors, *Size- and Age-Related Changes in Tree Structure and Function*, Tree Physiology, pages 255–286. Springer Netherlands, Dordrecht.

Meakem, V., Tepley, A. J., Gonzalez-Akre, E. B., Herrmann, V., Muller-Landau, H. C., Wright, S. J., Hubbell, S. P., Condit, R., and Anderson-Teixeira, K. J. (2018). Role of tree size in moist tropical forest carbon cycling and water deficit responses. *New Phytologist*, 219(3):947–958.

Medeiros, C. D., Scoffoni, C., John, G. P., Bartlett, M. K., Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C., and Sack, L. (2019). An extensive suite of functional traits distinguishes Hawaiian wet and dry forests and enables prediction of species vital rates. *Functional Ecology*, 33(4):712–734.

NEON (2018). National Ecological Observatory Network. 2016, 2017, 2018. Data Products: DP1.00001.001, DP1.00098.001, DP1.00002.001. Provisional data downloaded from http://data.neonscience.org/ in May 2019. Battelle, Boulder, CO, USA.

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., León-Gómez, C., Dawson, T., Martínez, J. J. C., Castorena, M., Echeverría, A., Espinosa, C. I., Fajardo, A., Gazol, A., Isnard, S., Lima, R. S., Marcati, C. R., and Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences*, 115(29):7551–7556.

Powell, T. L., Wheeler, J. K., Oliveira, A. A. R. d., Costa, A. C. L. d., Saleska, S. R., Meir, P., and Moorcroft, P. R. (2017). Differences in xylem and leaf hydraulic traits explain differences in drought tolerance among mature Amazon rainforest trees. *Global Change Biology*, 23(10):4280–4293.

Pretzsch, H., Schütze, G., and Biber, P. (2018). Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest Ecosystems*, 5(1):20.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rodríguez-Catón, M., Villalba, R., Srur, A. M., and Luckman, B. (2015). Long-term trends in radial growth associated with Nothofagus pumilio forest decline in Patagonia: Integrating local- into regional-scale patterns. *Forest Ecology and Management*, 339:44–56.

Rosas, T., Mencuccini, M., Barba, J., Cochard, H., Saura-Mas, S., and Martínez-Vilalta, J. (2019). Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. *New Phytologist*, 223(2):632–646.

Roskilly, B., Keeling, E., Hood, S., Giuggiola, A., and Sala, A. (2019). Conflicting functional effects of xylem pit structure relate to the growth-longevity trade-off in a conifer species. *PNAS. doi: /10.1073/pnas.1900734116.*

Ryan, M. G., Phillips, N., and Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment*, 29(3):367–381.

Sapes, G., Roskilly, B., Dobrowski, S., Maneta, M., Anderegg, W. R. L., Martinez-Vilalta, J., and Sala, A. (2019). Plant water content integrates hydraulics and carbon depletion to predict drought-induced seedling mortality. *Tree Physiology*, 39(8):1300–1312.

Scharnweber, T., Heinze, L., Cruz-García, R., van der Maaten-Theunissen, M., and Wilmking, M. (2019). Confessions of solitary oaks: We grow fast but we fear the drought. *Dendrochronologia*, 55:43–49.

Schöngart, J., Bräuning, A., Barbosa, A. C. M. C., Lisi, C. S., and de Oliveira, J. M. (2017). Dendroecological Studies in the Neotropics: History, Status and Future Challenges. In Amoroso, M. M., Daniels, L. D., Baker, P. J., and Camarero, J. J., editors, *Dendroecology: Tree-Ring Analyses Applied to Ecological Studies*, Ecological Studies, pages 35–73. Springer International Publishing, Cham.

Scoffoni, C., Vuong, C., Diep, S., Cochard, H., and Sack, L. (2014). Leaf Shrinkage with Dehydration: Coordination with Hydraulic Vulnerability and Drought Tolerance. *Plant Physiology*, 164(4):1772–1788.

Simeone, C., Maneta, M. P., Holden, Z. A., Sapes, G., Sala, A., and Dobrowski, S. Z. (2019). Coupled ecohydrology and plant hydraulics modeling predicts ponderosa pine seedling mortality and lower treeline in the US Northern Rocky Mountains. *New Phytologist*, 221(4):1814–1830.

Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D., and Knapp, A. K. (2019). How ecologists define drought, and why we should do better. *Global Change Biology*, 0(0):1–8.

Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018a). Assessing terrestrial laser scanning for developing non-destructive biomass allometry. *Forest Ecology and Management*, 427:217–229.

Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018b). Terrestrial LiDAR-derived non-destructive woody biomass estimates for 10 hardwood species in Virginia. *Data in Brief*, 19:1560–1569.

Stovall, A. E. L., Shugart, H., and Yang, X. (2019). Tree height explains mortality risk during an intense drought. *Nature Communications*, 10(1):1–6.

Suarez, M. L., Ghermandi, L., and Kitzberger, T. (2004). Factors predisposing episodic drought-induced tree mortality in Nothofagus– site, climatic sensitivity and growth trends. *Journal of Ecology*, 92(6):954–966.

Sørensen, R., Zinko, U., and Seibert, J. (2006). On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences*, 10(1):101–112.

Trenberth, K. E., Dai, A., van der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., and Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, 4(1):17–22.

666 Zuleta, D., Duque, A., Cardenas, D., Muller-Landau, H. C., and Davies, S. J. (2017). Drought-induced

667 mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon. *Ecology*,

668 98(10):2538–2546.